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Ocean warming, marine heatwaves and phytoplankton biomass: Long-term trends in the Northern Adriatic Sea

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ABSTRACT

In the present study, we investigated the trends of Sea Surface Temperature (SST), marine heatwaves (MHWs) and phytoplankton biomass, in terms of chlorophyll-*a* (chl-*a*), in the Northern Adriatic Sea (NAS), and the potential effects of ocean warming onto chl-*a*. Deseasonalized trends, calculated to assess the general tendencies without the effect of seasonality, showed a general increase of SST, and a decrease of chlorophyll-*a* concentration in almost the entire NAS. The strongest increase in SST was found along the eastern coast and in offshore areas, whereas the most pronounced decrease in chl-*a* was observed along the western coast, especially near the Po River delta. Seasonally, these trends were generally more marked in spring and summer. Spatial and seasonal variability in MHWs mean values and trends were also observed across the basin. A different response of chl-*a* to SST anomalies was highlighted over time, with negative correlations spreading throughout the NAS at subsequent time (one month later), together with positive correlations in eutrophic lagoonal areas. Different case studies and cluster analysis were used to assess the effects of ocean warming, also related to MHWs, on phytoplankton biomass. The relationships varied based on the background trophic conditions: in oligotrophic regions, marine heatwaves and extreme heat conditions led to reduced chlorophyll-*a* concentrations, while the same conditions in eutrophic areas, such as the western coast and lagoons, caused an increase in phytoplankton biomass. Our results indicated that MHWs and SST increases, are among the factors that are affecting the phytoplankton communities of the NAS.

1. Introduction

Ocean warming is considered one of the most threatening phenomena for marine ecosystems and society, contributing to a wide range of changes, such as sea level rise (Nerem et al., 2018), hydrological cycle alterations (Cheng et al., 2023; Durack et al., 2012), changes in ocean circulation (Caesar et al., 2018; Cheng et al., 2022), in stratification and overturning with consequences on nutrients and dissolved gases distribution (Stramma and Schmidtko, 2021; Venegas et al., 2023), and

promotion of conditions for extreme weather events.

Among the latter, marine heatwaves (MHWs) are generally defined as anomalously warm water events, with temperature higher than typical values, and persisting for a certain period of time. These events can be triggered by different atmospheric and/or oceanographic processes, from local and regional to large-climate scales and teleconnections (Behrens et al., 2019; Bian et al., 2023; Dalsin et al., 2023; Heidemann and Ribbe, 2019; Holbrook et al., 2019; Ibrahim et al., 2021; Sen Gupta et al., 2020; Vogt et al., 2022).

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The increase of sea water temperature and the marine heatwaves are exerting several huge impacts on the marine communities, like coral reefs (Le Nohaïc et al., 2017; Wyatt et al., 2023), birds (Jones et al., 2023; Piatt et al., 2020), zooplankton (Evans et al., 2020), fish (Free et al., 2023), top predators (Welch et al., 2023), seagrasses and habitat-forming species (e.g. Michaud et al., 2022; Serrano et al., 2021; Smale et al., 2019; Smale and Wernberg, 2013; Stipcich et al., 2022), with effects varying from individual to ecosystem levels, ranging from physiological adjustments and processes to mortality (Smith et al., 2023).

Despite their importance in the marine ecosystems (Blanchard et al., 2012; Khatiwala et al., 2009; Naselli-Flores and Padisák, 2023; Tweddle et al., 2018; Vallina and Simó, 2007), the effects on phytoplanktonic communities are inadequately explored. Several studies have shown that the response of chlorophyll-*a* (chl-*a*) to MHWs occurrence changes depending on both latitude and trophic conditions, with an increasing of chl-*a* concentration at high latitudes and in nutrient-rich waters, and a decreasing of chl-*a* concentration at mid-low-latitudes and in more oligotrophic waters (Hayashida et al., 2020; Le Grix et al., 2021; Montie et al., 2020; Noh et al., 2022; Sen Gupta et al., 2020).

The Mediterranean Sea is highly sensitive to climate change, and marine heatwaves are projected to increase in the early future (Darmaraki et al., 2019; Diffenbaugh et al., 2007; Giorgi, 2006; Lionello and Scarascia, 2018; Pisano et al., 2020). Several studies have observed an increase in MHWs frequency, duration and intensity in the entire Mediterranean Sea (Hamdeno and Alvera-Azcaráte, 2023; Ibrahim et al., 2021; Juza et al., 2022; Kuglitsch et al., 2010; Simon et al., 2022). Additionally, a negative relationship between Sea Surface Temperature Anomaly (associated with MHWs) and chl-*a* has been reported (Hamdeno and Alvera-Azcaráte, 2023), particularly with intense and long MHWs, and more in the Western than the Eastern Mediterranean. Moreover, Soulié et al. (2023) observed, through mesocosm studies in the Thau lagoon, that MHWs led to changes in phytoplankton physiological processes and in the phytoplankton community structure.

Most of the studies focusing on the effects of MHWs on phytoplankton are related to global or large scales. However, phytoplankton abundances, mean annual cycle and species composition show a strong variability on seasonal, interannual and spatial scales. An example is given by the Northern Adriatic Sea (NAS), where marked differences in terms of phytoplankton abundance, biomass and composition are found between coastal and offshore waters (Neri et al., 2022, 2023) and among different areas of the basin, like lagoons, eastern and western coasts (Bernardi Aubry et al., 2021, 2022; Cabrini et al., 2012; Marić et al., 2012; Totti et al., 2019; Vascotto et al., 2021). The NAS is a heterogeneous basin characterized by a shallow-depth, high riverine inputs (mainly from the Po River in the western area of the NAS) and a dominant surface cyclonic circulation with the Western Adriatic Current (WAC) flowing southward along the western coasts and bringing fresher and nutrient-rich waters from the northern areas, and the northward Eastern Adriatic Current, which brings saltier and more oligotrophic waters from the Ionian Sea along the eastern coast into the Adriatic Sea (Artegiani et al., 1997b; Poulain and Cushman-Roisin, 2001). Moreover, the NAS represents the area of generation of the North Adriatic Dense Water, the densest water mass in the Mediterranean Sea involved in the formation of the Adriatic Deep Water, which in turn influences the thermohaline circulation and water mass properties of the entire Mediterranean Sea (Gačić et al., 2001; Malanotte-Rizzoli et al., 1997; Zor-e-Armanda, 1963). Its unique hydrological and trophic characteristics support high productivity, biodiversity and variety of economically significant marine resources, such as for fisheries and aquaculture (Furlan et al., 2019; Veneroni and Jacobsen, 2024).

This hydrological and physico-chemical variability of the NAS contributes to significant trophic gradients across the NAS, with more eutrophic conditions prevailing in the northwestern areas, and oligotrophic conditions along the eastern and southern regions (Grilli et al., 2020). However, at the same time, the combined effects of riverine

inputs, circulation dynamics, shallow depths, and wind patterns renders it highly susceptible to climate change and ocean warming, as previously observed for the entire Adriatic Sea, with potential consequences on the phytoplankton communities, the food web and, consequently, on economic activities (Grbec et al., 2019). Therefore, the NAS acts as a natural laboratory where the impacts of climate events can be observed and analysed.

The aim of this study was to highlight the trends of temperature and chl-*a* (considered as a proxy of phytoplankton biomass) and to analyse the effect of some of the factors that could potentially influence phytoplankton biomass, i.e., ocean warming and marine heatwaves (as a measure of total heat stress), in the Northern Adriatic Sea.

2. Materials and methods

2.1. Study area and datasets

The study area is the entire NAS sub-basin, considering as its lower limit the latitude corresponding to 100 m isobath (Artegiani et al., 1997a) (Fig. 1).

Sea Surface Temperature values (SST, °C) from January 1, 1982 to December 31, 2023 were taken from the Copernicus Marine Service (CMEMS, <https://marine.copernicus.eu/>). The CMEMS Reprocessed (REP) Mediterranean (MED) dataset (DOI:10.48670/moi-00173; Merchante et al., 2019; Pisano et al., 2016; Saha et al., 2018) consists of daily and optimally interpolated satellite-based estimates of SST at 0.05° resolution grid.

Daily chlorophyll-*a* concentration (chl-*a*, mg m⁻³) was obtained from CMEMS, where the data were available since the end of 1997. The period from January 1, 1998 to December 31, 2023 was selected. The dataset (<https://doi.org/10.48670/moi-00299>) have a resolution of 1 ×

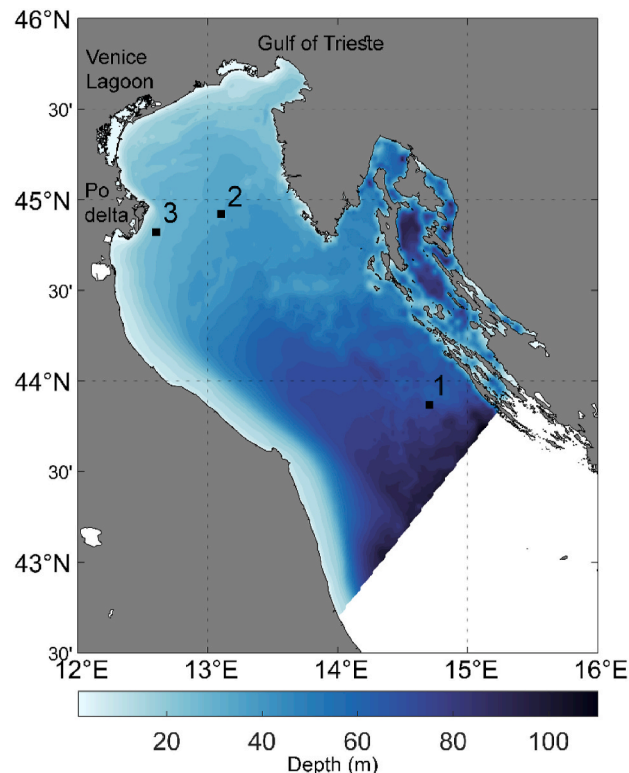


Fig. 1. Map of the study area, including bathymetry. Black rectangles correspond to the selected case studies: point 1, located off the eastern coast and more oligotrophic than the western and northern areas, point 2, situated off the Po River delta, and point 3, located south of the Po River delta. The years 2018, 2003, 2017 were considered in area 1, 2 and 3, respectively.

1 km and was evaluated through region-specific algorithms (Berthon and Zibordi, 2004; Volpe et al., 2019). For both SST and chl-*a*, the Northern Adriatic data were extracted from the Mediterranean datasets.

The maps showing the average values for the considered periods, i.e. 1982–2023 for SST and 1998–2023 for chl-*a*, are provided in Fig. S1A and B, respectively.

2.2. Marine heatwaves (MHWs)

MHWs were defined, following the definition of Hobday et al. (2016) as an event lasting at least five consecutive days where SST exceeds the variable 90th percentile threshold based on a 30-year climatological mean (1982–2012). Two consecutive MHW events within two days were considered as a unique event (Hobday et al., 2016). MHWs events were calculated (from January 1, 1982 to December 31, 2023) on a seasonal basis, and seasons were defined as follow: winter from January to March, spring from April to June, summer from July to September, autumn from October to December. For each season, MHWs were described by frequency (number of events y^{-1}), duration (duration of the event in days), days (sum of MHW days y^{-1}) and mean ($^{\circ}C$), maximum ($^{\circ}C$) and cumulative intensity ($^{\circ}C.days$), i.e. the integrated sea surface anomaly during the event, as defined by Hobday et al. (2016, 2018).

The MATLAB M_MHW toolbox v. 1.0 was used for MHW metric calculation (Zhao and Marin, 2019).

2.3. Data analyses

For both Sea Surface Temperature (SST, 1982–2023) and chlorophyll-*a* concentration (chl-*a*, 1998–2023), a seasonal decomposition was first applied to the monthly time series, using a 12-month cycle, to remove the seasonal component. Linear trends were then calculated on the deseasonalized data. Functions for trend calculation and deseasonalization were obtained from the Climate Data Toolbox (Greene et al., 2019).

For each season, linear trends of anomalies were calculated by subtracting the historical climatological mean at each grid point from the seasonal mean of SST and chl-*a* for each year of the time series. Seasons were considered as follow: January–March as winter, April–June as spring, July–September as summer, October–December as autumn, as previously done in other studies (Bernardi Aubry et al., 2006; Grilli et al., 2020; Neri et al., 2022, 2023).

Moreover, to assess the presence of overall seasonal trends in the entire NAS of SST, chl-*a* concentration and MHW metrics, the Mann-Kendall test (Kendall, 1975; Mann, 1945) was performed. The test returns Kendall's τ coefficient, which indicates the direction and persistency of the trend, with values ranging from -1 to $+1$ (indicating a strong decreasing and increasing trend, respectively).

For the following analyses, the same time interval (i.e., 1998–2023) was considered for both SST and chl-*a* concentration. To investigate the effects of extreme heat conditions on the chl-*a* concentration, the 90th percentile of temperature values was considered as threshold to distinguish between two conditions in each season: extreme heat (values above the 90th percentile) and normal temperature (values between the 90th and the 10th percentile). K-means clustering (Lloyd, 1982; MacQueen, 1967) was performed seasonally to identify distinct spatial regions with similar chl-*a* concentration patterns across the two temperature conditions. The Elbow Method (Lloyd, 1982) was used to determine the optimal number of clusters (K), that was assessed as 3. In each cluster, a Wilcoxon rank sum test (equivalent to the Mann-Whitney U test) was performed to assess whether there were significant differences in chlorophyll-*a* concentrations between two temperature categories (i.e., extreme hot and normal).

To evaluate potential immediate and delayed responses of chl-*a* to SST anomalies, a lagged correlation analysis was performed over a range of temporal lags from 0 to 1 (i.e., from no lag to 1 month later). For each

spatial grid cell, the chl-*a* time series was shifted by the corresponding lag and Spearman correlations were calculated to test for lagged response of chl-*a*. Wilcoxon rank sum test was used for to test significance.

Moreover, to analyse the effects of MHWs (and the associated SST anomalies), three areas were selected as case studies (Fig. 1), considering the different trophic conditions of the NAS: the first area (point 1 in Fig. 1) was chosen off the eastern coast (more oligotrophic than the western and northern areas of the NAS), the second area (point 2 in Fig. 1) was chosen among the ones with intermediate characteristics between the first and the third area, which is highly affected by riverine inputs (point 3 in Fig. 1). In each point, a specific year was selected based on the MHW characteristics (Fig. S2) of the entire period (1982–2023): in point 1, 2018 was chosen due to a combination of MHW maximum intensity (5.56), frequency (7) and days (139) (Fig. S2A); in point 2 the 2003 was considered for the occurrence of the strongest MHWs (in late spring) (Fig. S2B); in point 3 the year 2017 was selected because of the strongest winter MHWs (Fig. S2C). For each case study, Spearman correlations were calculated between daily SST anomalies and daily chl-*a* values, considering the entire year and the selected MHW event (Fig. S2).

In the present study, the threshold for statistical significance was considered at $p < 0.05$.

MATLAB software was used for the analyses (The MathWorks Inc., Release R2022b).

3. Results

3.1. SST and chl-*a* trends

The deseasonalized SST and chl-*a* trends in the NAS are represented in Fig. 2A and B, respectively. Significant ($p < 0.001$) increases in SST and decreases in chl-*a* concentration were observed in the entire basin. SST trends ranged from $0.05\ ^{\circ}C\ y^{-1}$ along the eastern coast to $0.033\ ^{\circ}C\ y^{-1}$ in the northern and western coastal areas. Regarding the chl-*a* trends ($p < 0.05$), a strong spatial gradient was observed, with the strongest and the weakest decreases noticed along the western ($-0.13\ mg\ m^{-3}\ y^{-1}$) and the eastern coasts ($-0.0002\ mg\ m^{-3}\ y^{-1}$), respectively. Only in certain localized areas (e.g., in some points in lagoon of Venice, the lagoon of Grado and in semi-enclosed areas between the Croatian islands) an increasing trend of chl-*a* was observed (minimum = 0.0004 , maximum = $0.04\ mg\ m^{-3}\ y^{-1}$).

At a seasonal level, an overall increase of SST ($p < 0.001$) was observed in each season when the entire NAS was considered ($\tau = 0.43$ in winter, $\tau = 0.46$ in spring, $\tau = 0.47$ in summer, $\tau = 0.34$ in autumn). The highest increase of SST was found in spring (Fig. 3B, ranging from 0.046 to $0.084\ ^{\circ}C\ y^{-1}$) and summer (Fig. 3C, ranging from 0.034 to $0.058\ ^{\circ}C\ y^{-1}$), while in winter and autumn (Fig. 3A and D, respectively), similar increasing trends were observed (from 0.015 to 0.046 and from 0.016 to $0.041\ ^{\circ}C\ y^{-1}$ in winter and autumn, respectively). In both winter and autumn, no trend was observed along the western coasts ($p > 0.05$).

Considering the overall seasonal trends of chl-*a* in the NAS, decreasing trends were observed in winter ($\tau = -0.19$, $p < 0.05$), summer ($\tau = -0.16$, $p < 0.05$) and autumn ($\tau = -0.26$, $p < 0.001$), while in spring the decrease was not significant ($\tau = -0.08$, $p > 0.05$). Regarding the spatial distribution of chl-*a* seasonal anomalies, a variability was observed (Fig. S3). In winter ($p < 0.05$), the highest decrease ($-0.16\ mg\ m^{-3}\ y^{-1}$) was observed along the western coast below the Po River delta, followed by some scattered zones in the northernmost offshore area and in the Gulf of Trieste. In spring ($p < 0.05$), the highest decrease of chl-*a* was observed in front of the Po River delta ($-0.17\ mg\ m^{-3}\ y^{-1}$), followed by the Gulf of Trieste and in the eastern semi-enclosed areas. In summer ($p < 0.05$), the highest decrease of chl-*a* was found in front of the Po River delta ($-0.19\ mg\ m^{-3}\ y^{-1}$), along the northeastern coastal areas and in the coastal and offshore areas of the

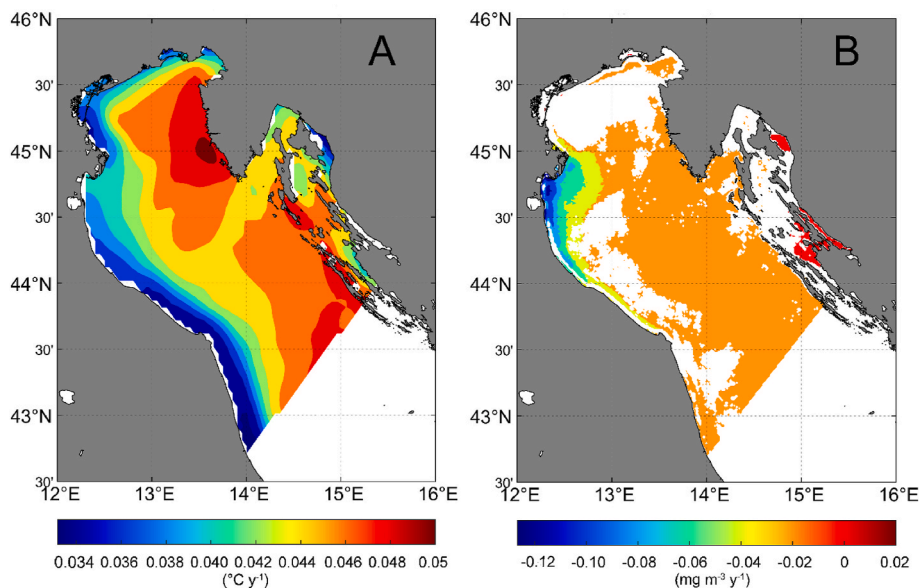


Fig. 2. Trends of deseasonalized Sea Surface Temperature ($^{\circ}\text{C y}^{-1}$, A) and chl-*a* concentration ($\text{mg m}^{-3} \text{y}^{-1}$, B). Blank areas not significant trends ($p > 0.05$).

lower subbasin. In autumn ($p < 0.05$), the decrease of chl-*a* was widespread throughout the NAS, with a gradient from the western coast, where the highest decrease was observed ($-0.06 \text{ mg m}^{-3} \text{y}^{-1}$), to the offshore areas and eastern coasts. Increasing trends of chl-*a* ($p < 0.05$) were found in winter and autumn in the eastern semi-enclosed areas ($0.01 \text{ mg m}^{-3} \text{y}^{-1}$ in both seasons) and in spring in the Lagoon of Venice ($0.08 \text{ mg m}^{-3} \text{y}^{-1}$).

3.2. Marine heatwaves (MHWs)

Maps of seasonal MHW metric mean values in the NAS are shown in Figs. 4–5. The highest values for MHW mean ($3.98 \text{ }^{\circ}\text{C}$), maximum ($7.76 \text{ }^{\circ}\text{C}$), and cumulative ($54.83 \text{ }^{\circ}\text{C.days}$) intensities (Fig. 4) were observed in spring. However, high values of MHW cumulative intensity (maximum = $51.85 \text{ }^{\circ}\text{C.days}$) were also recorded in winter along the northeastern and eastern coasts. High values of MHW mean frequency (Fig. 5) were found in summer almost in the entire basin (maximum = 1.10 number of events y^{-1}), although in some scattered areas high mean values were found even in different seasons (maximum in winter = 1.19 number of events y^{-1}). Considering mean duration and mean days (Fig. 5), the highest values were found in winter (maximum = 33.17 days and 20 days, respectively).

Considering the overall trends in the entire NAS (Table 1), frequency ($p < 0.001$), duration ($p < 0.05$), number of days ($p < 0.001$) and cumulative intensities ($p < 0.05$) showed increasing trend in each season, while mean and maximum intensities showed increasing trends only in summer ($p < 0.001$). The spatial maps of trends of seasonal MHW metric in the NAS are shown in Figs. S3–4.

3.3. Correlations between SST anomalies and chl-*a* values

The lagged correlation maps between SST anomalies and chl-*a* are shown in Fig. 6. At lag 0 (i.e., no time lag, Fig. 6A), significantly positive correlations ($p < 0.05$) were detected along the northernmost and western coast, while negative correlations ($p < 0.05$) were found along the eastern coast and eastern offshore area. After one month (1 lag, Fig. 6B), negative correlations ($p < 0.05$) are widespread throughout the Northern Adriatic Sea, except for the northernmost coastal and lagoonal areas, where positive correlations were consistently detected ($p < 0.05$).

3.4. Chlorophyll-*a* concentration in extreme and normal heat conditions

In each season, cluster analysis revealed three clusters (Fig. 7), with similar chl-*a* concentration patterns across the two temperature conditions (i.e. extreme and normal), dividing the NAS in three sub-areas: one spanning from the eastern coast, the northeastern area to the western offshore area (cluster 1), one from the Venice lagoon southward to the most coastal belt below the Po River delta (cluster 3), and one containing the remaining western area in between (cluster 2).

In cluster 1, in each season lower values of chl-*a* ($p < 0.001$) were found in extreme heat conditions than in normal ones (0.227 ± 0.006 and $0.416 \pm 0.009 \text{ mg m}^{-3}$ in winter, 0.234 ± 0.006 and $0.423 \pm 0.008 \text{ mg m}^{-3}$ in spring, 0.214 ± 0.004 and $0.394 \pm 0.008 \text{ mg m}^{-3}$ in summer, 0.256 ± 0.006 and $0.462 \pm 0.010 \text{ mg m}^{-3}$ in autumn). Similarly, in cluster 2, in each season lower values of chl-*a* ($p < 0.001$) were found in extreme heat conditions than in normal ones (1.586 ± 0.044 and $2.170 \pm 0.037 \text{ mg m}^{-3}$ in winter, 1.704 ± 0.050 and $2.181 \pm 0.039 \text{ mg m}^{-3}$ in spring, 1.492 ± 0.039 and $2.108 \pm 0.036 \text{ mg m}^{-3}$ in summer, 2.222 ± 0.071 and $2.624 \pm 0.051 \text{ mg m}^{-3}$ in autumn). On the contrary, in cluster 3 higher values of chl-*a* were observed in conditions of extreme heat than in the normal ones (5.8093 ± 0.32275 and $5.441 \pm 0.235 \text{ mg m}^{-3}$ in winter, 6.3323 ± 0.34049 and $5.275 \pm 0.213 \text{ mg m}^{-3}$ in spring, 5.3551 ± 0.28266 and $5.342 \pm 0.191 \text{ mg m}^{-3}$ in summer and 8.6788 ± 0.61936 and $6.750 \pm 0.275 \text{ mg m}^{-3}$ in autumn), although the differences were significant only in spring and autumn ($p < 0.05$).

3.5. Case studies

Fig. 8 shows the time series of daily SST anomalies ($^{\circ}\text{C}$, red line) and daily log chl-*a* concentration (mg m^{-3} , green line) during 2018 (point 1, A), 2003 (point 2, B), 2017 (point 3, C), while the MHW events in the selected years and areas are represented in Fig. S1.

Considering the entire selected years, negative correlations between SST anomalies and chl-*a* values were found in point 2 ($\rho = -0.29$, $p < 0.001$) and in point 1 ($\rho = -0.14$, $p < 0.01$), while positive correlations were found in point 3 ($\rho = 0.28$, $p < 0.001$). Considering the SST anomalies during the MHW events (Fig. 8), in point 1, negative correlations were found between the SST anomalies and chl-*a* during the spring MHW event. In point 2, positive correlations ($\rho = 0.09$) were found between the SST anomalies of the late spring MHW event and chl-*a*, although not significant ($p > 0.05$). In point 3, positive correlations were found when the winter MHW was considered ($\rho = 0.51$, $p <$

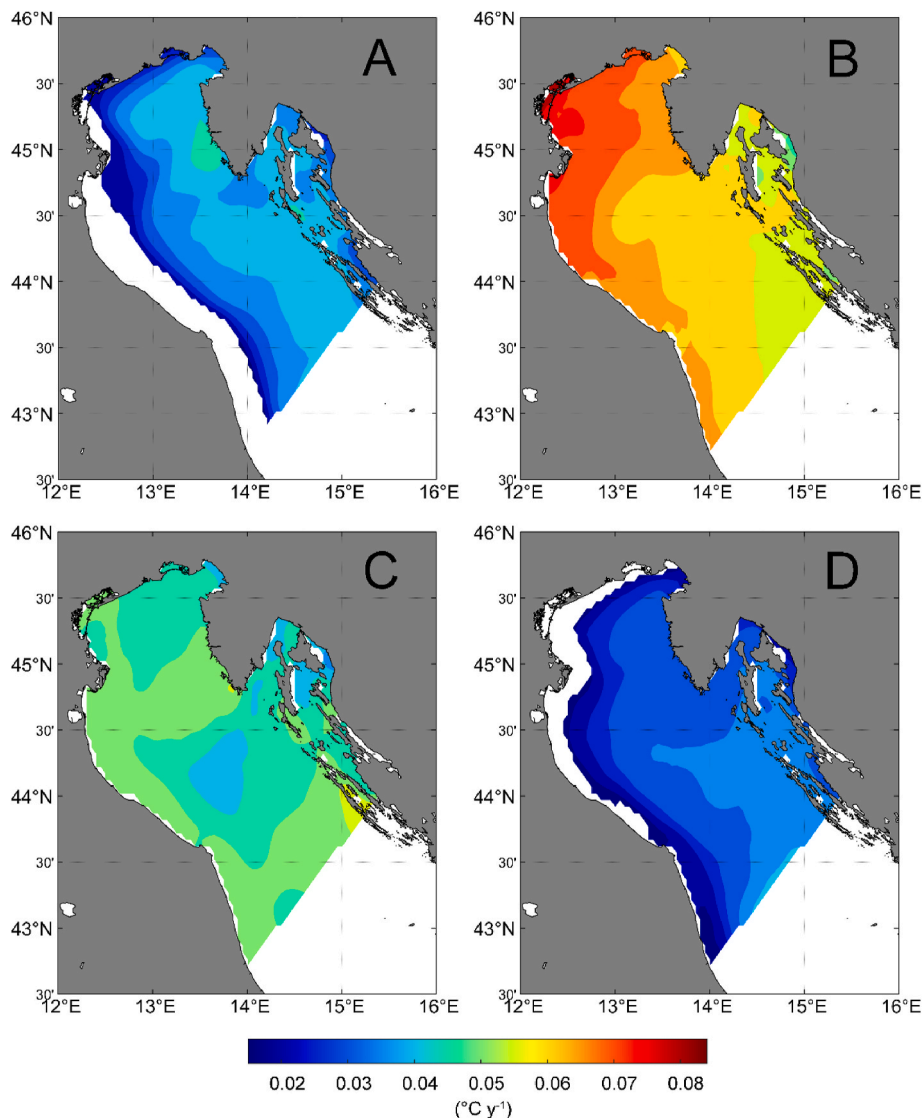


Fig. 3. Trends of seasonal anomalies of Sea Surface Temperature ($^{\circ}\text{C y}^{-1}$): winter (A), spring (B), summer (C) and autumn (D). Blank points represent $p > 0.05$.

0.01).

4. Discussion

In this study we highlighted that ocean warming and marine heatwaves are among those factors affecting phytoplankton biomass in the Northern Adriatic Sea, with differences depending on the background conditions.

The observed increasing of Sea Surface Temperature (SST) in the entire NAS in the period 1982 to 2023 is in agreement with that already documented in the Adriatic and in the rest of the Mediterranean Sea, with values ranging from 0.038 to 0.05 $^{\circ}\text{C y}^{-1}$ (Hamdeno and Alvera-Azcarate, 2023; Ibrahim et al., 2021; Mohamed et al., 2019; Pastor et al., 2018, 2020; Pisano et al., 2020). The increasing is not homogenous over the year, but it has a clear seasonal dependence, as the spring (April–June) showed the highest increase, followed by summer (July–September), while the lowest increase was found in autumn or winter. This variability was also reported by other studies in the Mediterranean Sea, which related the seasonal and spatial variabilities of SST increase to circulation, mean air-sea heat fluxes, ocean processes (e.g., advection and vertical mixing of heat) and changes in large scale modes of atmospheric variability as the North Atlantic Oscillation (López García and Camarasa Belmonte, 2011; Pisano et al., 2020; Skliris et al.,

2012). We assume that the NAS is influenced by similar processes, in addition to the varying contributions of riverine inputs and water column depth, which differentially affect the various regions of the basin.

Recent studies have highlighted that the increasing trend of temperature itself could influence the observed trend of occurrence and metrics (i.e. frequency, intensities and duration) of MHWs (Amaya et al., 2023; Martínez et al., 2023; Xu et al., 2022), which explains the high values and increasing trend of MHW metrics that we observed in spring and summer. Anyway, other factors rather than SST, such as atmospheric pressure and winds, influence MHW assessments (Sen Gupta et al., 2020), contributing to the observed high spatial and seasonal variability in MHW metric trends (Figs. S4–5), which do not always align with those of SST. The lack of observable trends or the presence of negative trends in the MHW metrics may also be related to an intrinsic limit to the increase in SST, which can rise to a maximum value related to the maximum amount of heat that the atmosphere releases to the sea. If this condition is repeated over the years, the anomaly will vary minimally, leading to decreased or even absent trends, and further increases may not be easily detectable. This suggests that a re-definition of MHWs should be considered, although this aspect warrants further investigation. Anyway, recently, Martínez et al. (2023) claimed that, when the effects of marine heatwaves on the ecosystems are addressed, the combined marine heatwave and temperature trend (i.e. total heat

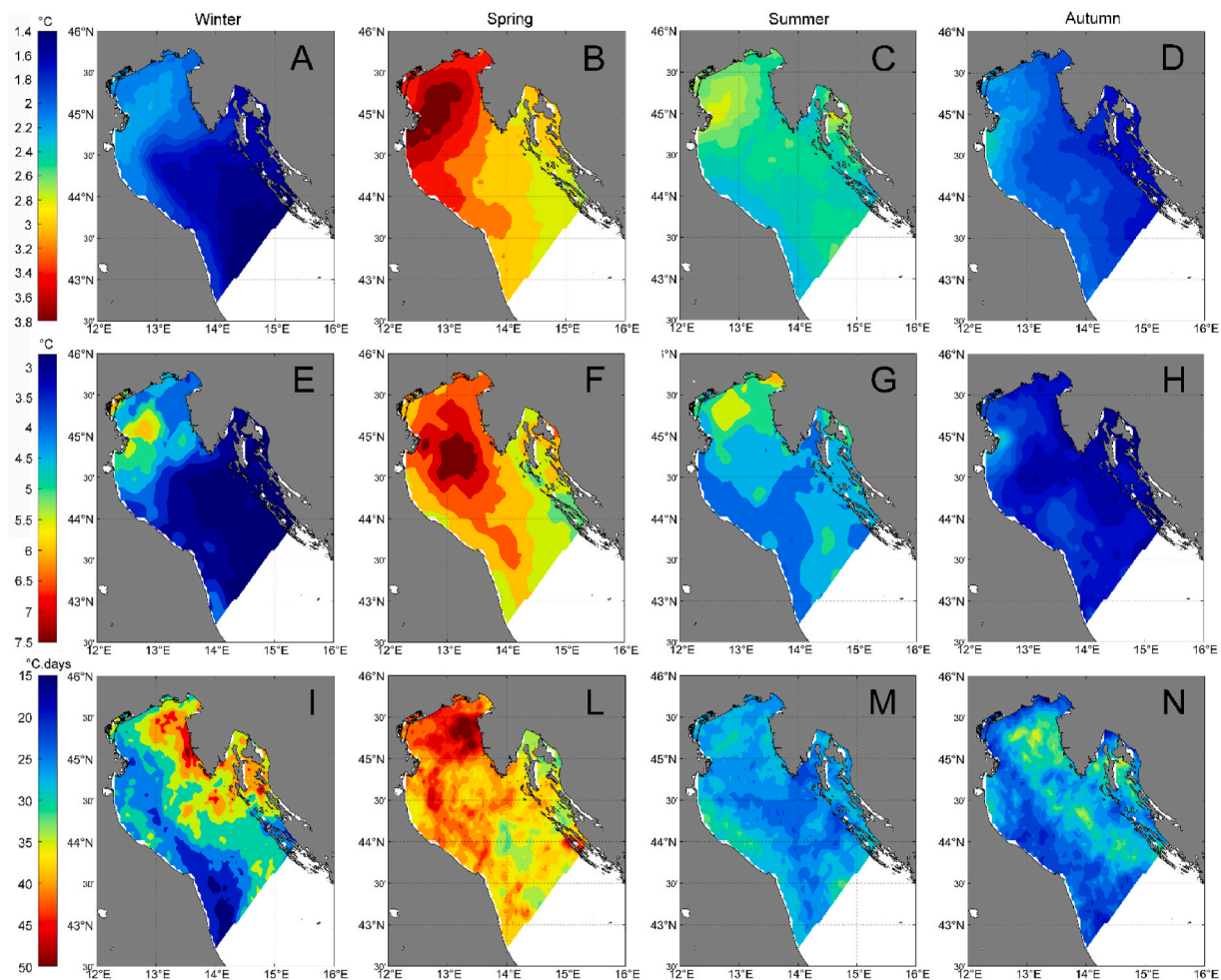


Fig. 4. Mean values of marine heatwave metrics: mean intensities ($^{\circ}\text{C}$) (A, B, C, D), max intensities ($^{\circ}\text{C}$) (E, F, G, H) and cumulative intensities ($^{\circ}\text{C}\cdot\text{days}$) (I, L, M, N) in winter (A, E, I), spring (B, F, L), summer (C, G, M) and autumn (D, H, N).

exposure/stress) should be considered. Indeed, regardless of the definition and calculation of the marine heatwave trends, previous studies highlighted, at a global scale, negative relationships between MHWs and phytoplankton biomass (i.e. chl-*a*), particularly at low and mid-latitudes (Noh et al., 2022; Sen Gupta et al., 2020), and that these relationships are influenced by the background nutrient and circulation conditions (Chauhan et al., 2023; Hayashida et al., 2020).

Similarly, in our study, the importance of background conditions in modulating the impact of ocean warming and marine heatwaves was highlighted: in oligotrophic or mesotrophic conditions (e.g., in the eastern and offshore areas), extreme heat events were associated with lower chlorophyll-*a* levels, whereas the opposite pattern was observed in more eutrophic regions, such as lagoons and the western coast. Moreover, when the relationships between the SST anomalies associated to MHW events and chl-*a* values were analysed, negative and positive correlations were found in oligotrophic and eutrophic areas, respectively, accordingly to Hayashida et al. (2020).

~~Chl-*a* concentration showed a general decreasing trend in almost the entire Northern Adriatic Sea in the period 1998 to 2023, in agreement with the future projections recently reported by Mentaschi et al. (2024). These results suggest that the trend towards oligotrophication, observed in the years 2000–2007 (Colella et al., 2016; Giani et al., 2012; Marić et al., 2012; Mozetić et al., 2010) and apparently reversed in the 2010s (Cozzi et al., 2020; Kotta and Kitsiou, 2019; Salgado-Hernanz et al., 2019; Totti et al., 2019), has been re-established. However, the decrease in phytoplankton biomass observed in our study (with the only exception in the Venice Lagoon) varied between areas and among seasons. In~~

~~autumn, a slight decrease was observed widespread in almost the entire basin, in agreement with Grilli et al. (2020), although they considered a different period (1971–2015), while in winter it was recorded in the Gulf of Trieste and in the western coast, and in summer in the Gulf of Trieste, the western coast and the southern areas. The decreasing of chl-*a* concentration observed in winter has been already reported in other studies and related to the increasing of temperature and consequent phenomena, like changes in nutrient concentrations, and to positive North Atlantic Oscillation index (Borkman and Smayda, 2009; Cabrini et al., 2012; Cerino et al., 2019). These trends reflect the decreasing of the winter bloom, sustained in the NAS by small colonial diatoms (mainly *Skkeletonema marinoi*) and representing one of the most regular phenomena in the phytoplankton annual cycle of the NAS leading to the most significant biomass increase during the year (Bernardi Aubry et al., 2004; Totti et al., 2019).~~

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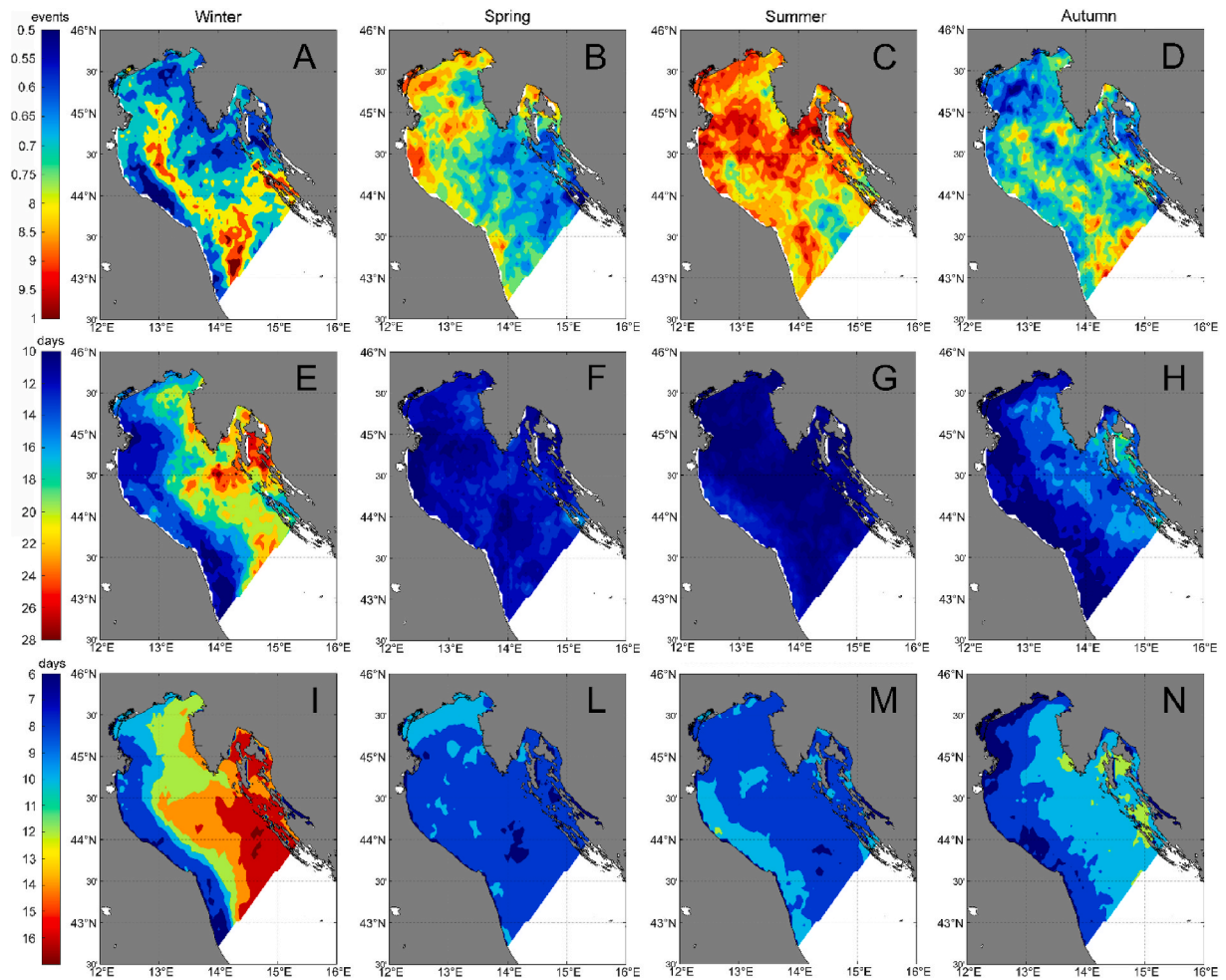


Fig. 5. Mean values of marine heatwave metrics: frequency (events) (A, B, C, D), duration (days) (E, F, G, H) and days (days) (I, L, M, N) in winter (A, E, I), spring (B, F, L), summer (C, G, M) and autumn (D, H, N).

Table 1

Results of the Mann-Kendall test (Kendall’s τ coefficient) of the marine heatwaves frequency (number of events), duration (duration of the event in days), days (sum of MHW days) and mean (MeanInt, °C), maximum (MaxInt, °C) and cumulative intensity (CumInt, °C.days) (mean, maximum and integrated sea surface anomaly during/over the event) in the entire NAS. Values in bold, bold and italic, bold italic and underlined represent $p < 0.05$, 0.01 and 0.001 , respectively.

Season	Frequency (τ , events)	Duration (τ , days)	MeanInt (τ , °C)	MaxInt (τ , °C)	CumInt (τ , °C. days)	Days (τ , days)
Winter	<u>0.44</u>	<u>0.46</u>	0.05	0.14	<u>0.35</u>	<u>0.46</u>
Spring	<u>0.49</u>	<u>0.30</u>	0.05	0.15	<u>0.24</u>	<u>0.49</u>
Summer	<u>0.58</u>	<u>0.35</u>	<u>0.42</u>	<u>0.46</u>	<u>0.40</u>	<u>0.53</u>
Autumn	<u>0.35</u>	<u>0.16</u>	-0.02	0.11	<u>0.30</u>	<u>0.37</u>

different period (1971–2015). In winter, a decrease was recorded in the Gulf of Trieste and along the western coast, while in summer, it was observed in the Gulf of Trieste, the western coast, and southern areas. The decreasing of chl-*a* concentration observed in winter has been already reported in other studies and related to the increasing of temperature and consequent phenomena, like changes in nutrient concentrations, and to a positive North Atlantic Oscillation index (Borkman and Smayda, 2009; Cabrini et al., 2012; Cerino et al., 2019). These trends reflect the decreasing of the winter bloom, sustained in the NAS by small colonial diatoms (mainly *Skeletonema marinoi*) and representing one of the most regular phenomena in the phytoplankton annual cycle of the

NAS leading to the most significant biomass increase during the year (Bernardi Aubry et al., 2004; Totti et al., 2019).

These findings align with previous studies related to long-term ecological changes in the Northern Adriatic Sea, where phytoplankton biomass and community structure have undergone significant inter-decadal variability. This variability has been driven by both anthropogenic impacts, such as reduced nutrient loading due to wastewater treatment and changes in agricultural practices, and climate-related drivers, including river discharge variability and large-scale atmospheric patterns (Bernardi Aubry et al., 2004; Giani et al., 2012; Mozetič et al., 2010; Cozzi et al., 2020). Notably, the transition from eutrophic to oligotrophic conditions since the early 2000s has been accompanied by a shift in phytoplankton composition, a reduction in bloom intensity, and some mucilage events (Totti et al., 2019; Marić et al., 2012). Our results, particularly the generalized decline in chl-*a* concentrations during spring and summer, reinforce this trajectory and suggest that ocean warming and marine heatwaves may act synergistically with reduced nutrient availability, further constraining phytoplankton productivity in the NAS. These decreases of chl-*a* concentration may be partly explained by a direct effect of temperature on phytoplankton species ecophysiology, considering that previous studies have highlighted that higher temperatures could imbalance the ratio between photosynthesis and respiration, favouring the latter with a potential biomass decrease (Boscolo-Galazzo et al., 2018; O’Connor et al., 2009). However, they could be also related to the effects that the increasing of sea water temperatures and of marine heatwave metrics exert toward the oceanographic conditions (e.g. longer period of stratification preventing the

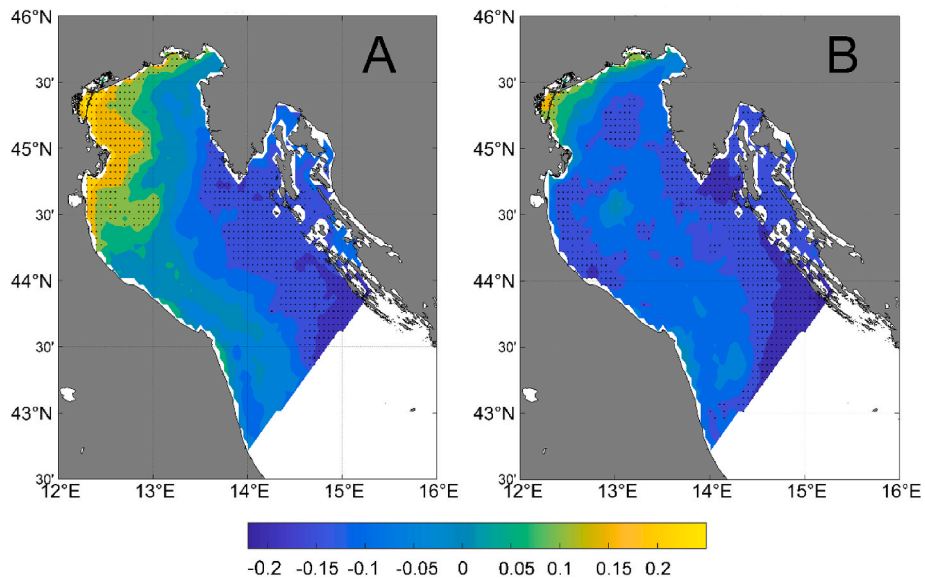


Fig. 6. Map representing the lagged correlations between monthly Sea Surface Temperature anomalies ($^{\circ}\text{C}$) and chl-*a* values (mg m^{-3}). Dots represent significant correlations ($p < 0.05$).

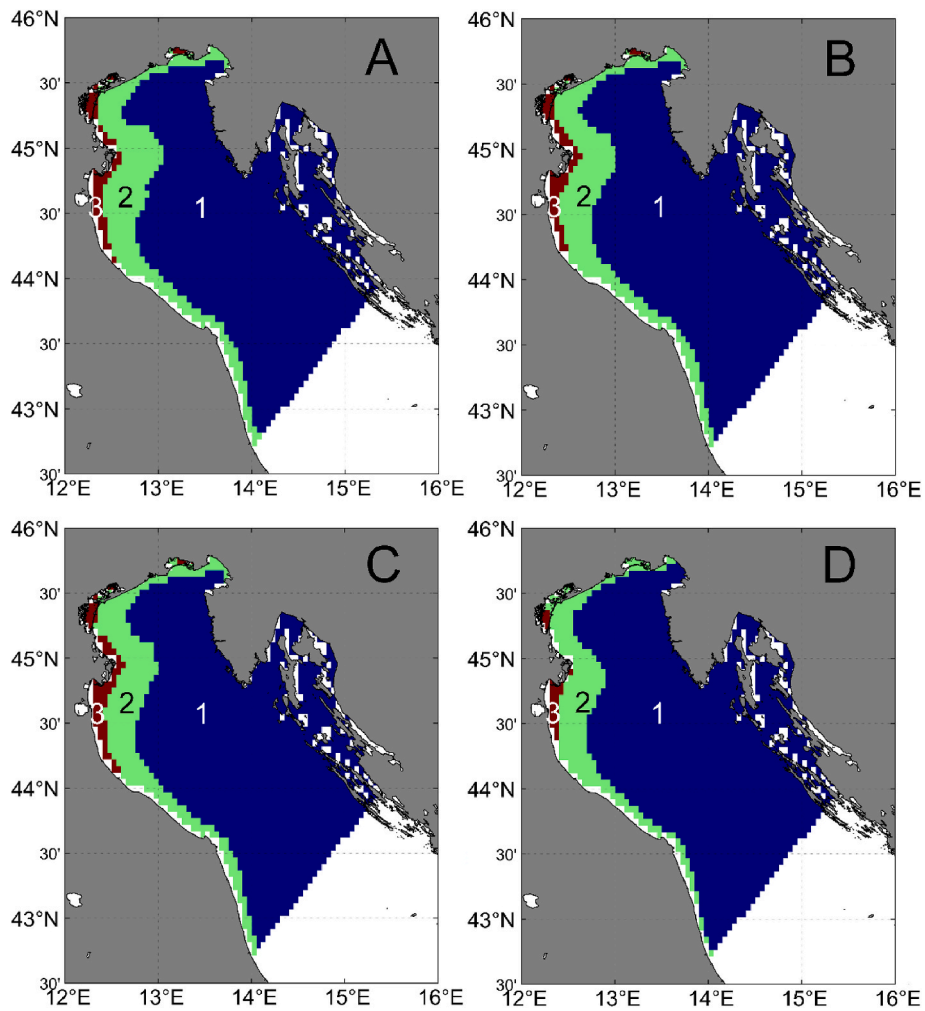


Fig. 7. Clusters of the Northern Adriatic Sea resulting from the cluster analysis, in winter (A), spring (B), summer (C) and autumn (D). Colours and numbers represent the distinct clusters: dark blue (cluster 1), green (cluster 2), red (cluster 3).

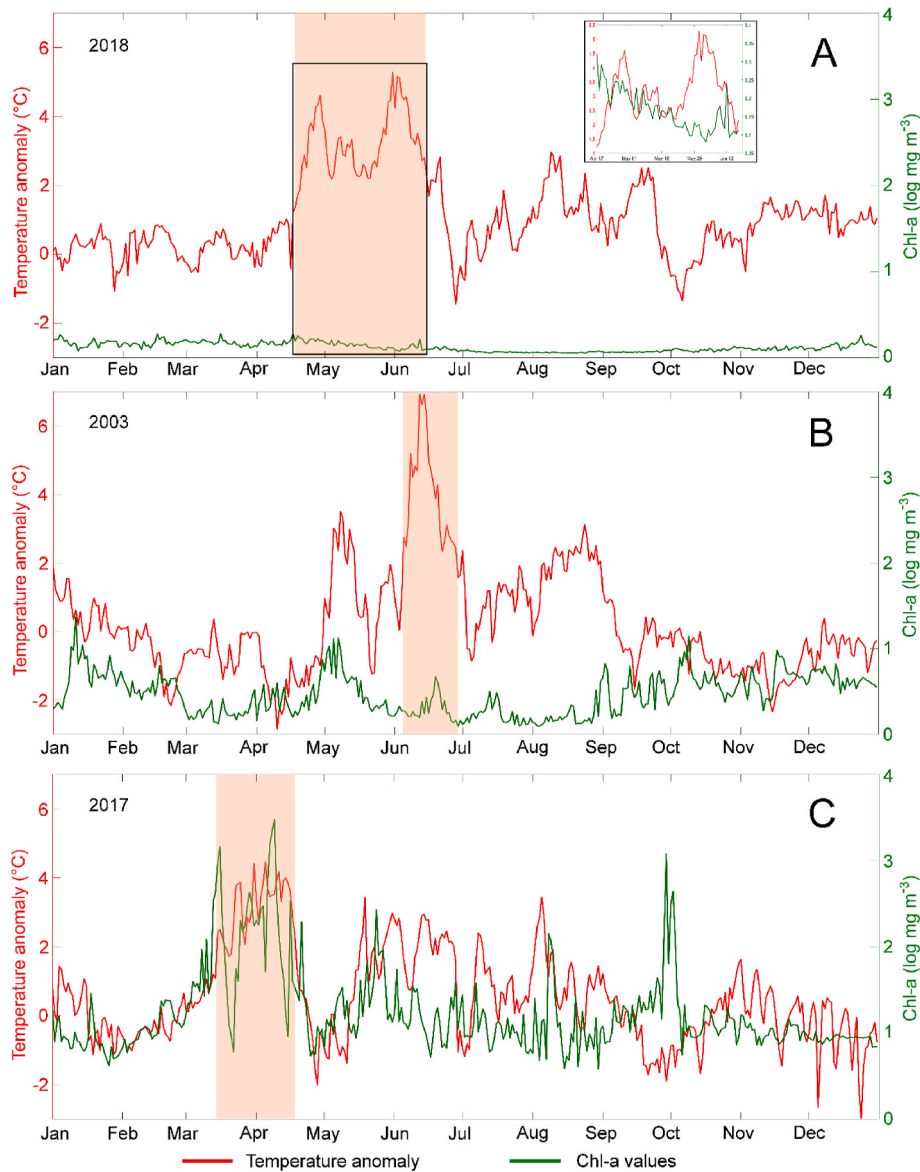


Fig. 8. Time series of daily Sea Surface Temperature anomalies ($^{\circ}\text{C}$, red line) and daily log chl-*a* concentration (mg m^{-3} , green line) during 2018 (point 1, A), 2003 (point 2, B), and 2017 (point 3, C). The orange shaded areas indicate the MHW events included in the case studies. Due to the generally low values in point 1 (A), a zoomed-in view of these values during the MHWs is presented in the upper-right inset.

mixing of the water column), and the physical and chemical characteristics of seawater, as found for other climatic processes (Leterme et al., 2005; Ninčević Gladan et al., 2010).

Considering each season separately, decreasing trends of chl-*a* were not always found, even if increasing trends of temperature/MHWs were observed. This could be explained considering that other crucial factors, such as changes in nutrient loadings and balance related to the reduction of the river discharge (mainly the Po River) and to the alternation of very dry and very wet periods (Cavallini et al., 2024), are likely negatively related to phytoplankton biomass (Cibic et al., 2018).

However, the effect of SST warming on phytoplankton could be masked and changed on time, as highlighted by the lagged correlations, with negative correlations appearing later (one month in the present study). This effect is further enhanced when it is superimposed on other phenomena that contribute to the creation of a MHW, such as stratification and changes in wind intensities and air-sea heat fluxes (Holbrook et al., 2019; Sen Gupta et al., 2020; Vogt et al., 2022).

5. Conclusions

Sea Surface Temperature (SST) and marine heatwaves (MHWs) are increasing worldwide due to climate change. Their effects on the phytoplankton communities have often been studied at global scales. In the present study, the trends of SST, MHWs, chl-*a* and their potential relationships were analysed in Northern Adriatic Sea, a heterogeneous basin characterized by significant gradients of the main physical, chemical and biological parameters.

Increasing trends of SST (1982–2023) were observed in the entire Northern Adriatic Sea. The spatial and seasonal variability of MHW metrics did not always coincide with SST trends, indicating the influence of additional factors to SST in the establishment of MHW events.

The general decline in chlorophyll-*a* concentrations from 1998 to 2023 is an indicator of a tendency towards oligotrophication in the NAS. These decreases may be partly related to rising temperatures and associated changes in oceanographic conditions, such as prolonged stratification and altered nutrient dynamics. However, despite the clear influence of rising temperatures, the interpretation of the effects of

MHWs on the phytoplankton biomass is not easy, as many factors (more or less) temperature dependent (e.g. wind patterns, air-sea heat fluxes, water column stability, rain regime, river discharge, nutrients load) play crucial roles in shaping the local phytoplankton dynamics.

Overall, this study underscores the complex and multifaceted nature of ocean warming and marine heatwaves effects on phytoplankton biomass, emphasizing the need for continued monitoring and consideration of local studies to analyse the future changes and their potential effects in marine ecosystems.

CRedit authorship contribution statement

Francesca Neri: Data curation, Formal analysis, Investigation, Writing – original draft. **Angela Garzia:** Data curation, Formal analysis. **Marika Ubaldi:** Data curation, Formal analysis. **Tiziana Romagnoli:** Data curation. **Stefano Accoroni:** Conceptualization, Supervision, Writing – review & editing. **Alessandro Coluccelli:** Data curation, Formal analysis. **Annalisa Di Cicco:** Formal analysis, Writing – review & editing. **Francesco Memmola:** Data curation, Formal analysis. **Pierpaolo Falco:** Conceptualization, Supervision, Writing – review & editing. **Cecilia Totti:** Conceptualization, Supervision, Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jecss.2025.109282>.

Data availability

Data will be made available on request.

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